GENETICS OF THE FOWL. II.

A FOUR-GENE AUTOSOMAL LINKAGE GROUP[1]

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While the study of sex-linked genes in the fowl has proceeded in a very satisfactory manner, geneticists have experienced some difficulty in discovering linkage groups among the autosomes of that species. In this paper there are reported certain data on a case of autosomal linkage which, when considered along with the findings of other workers, permit the definite assignment of four genes to one linkage group and give some idea of their arrangement in the chromosome.

The literature on autosomal linkage in the fowl is so scanty that it may be briefly reviewed. A start in this direction was made when DUNN and JULL (1927) reported some evidence for the linkage of dominant white, cerebral hernia and polydactyly. Additional data presented by DUNN and LANDAUER (1930) made it clear that there is close linkage between the genes for the first two of these characters and suggested that polydactyly might be in the same chromosome but comparatively loosely linked with the other two. More extensive data obtained by WARREN (1932) show independent segregation of dominant white and polydactyly in a backcross progeny of 310 fowls.

Meanwhile SEREBROVSKY and PETROV (1928, 1930) reported linkage of creeper and rose comb, with crossing over of 9.1 percent in 297 progeny from diheterozygous males. A much closer linkage of these two genes was decisively demonstrated by LANDAUER (1931) who found only 0.45 percent of crossing over between them in 4483 backcross progeny.

SEREBROVSKY and PETROV (1930) postulated that creeper also belonged in the linkage group containing dominant white, but their evidence for such an assumption was hardly adequate and the possibility is disproved by the evidence (see table 6) for the independence of dominant white and rose comb. These investigators also present evidence that the genes for blue plumage color and bare neck may be linked.

More recently SUTTLE and SIPE (1932) have reported the finding of about 28 percent of crossing over between frizzling and crest. The data presented below show that frizzling is linked with dominant white. It therefore follows that dominant white, cerebral hernia, frizzling and crest are in one linkage group.

It must be pointed out that while a considerable number of linkage trials not reviewed above have shown only the independence of the genes tested, the possibility remains that certain pairs might be in one chromosome but too far apart to show any linkage. Thus WARREN (1932) has presented linkage-test data which, taken with some from the work of SEREBROVSKY and PETROV (1930), cover 35 of the 36 possible combinations in pairs of the following nine autosomal characters: naked neck, rumpless, white skin, dominant white, leg feathering, rose comb, pea comb, crest and poly-dactyly. All of these 35 trials showed independence. Since the fowl has (probably) 17 pairs of autosomes, one would expect to find by chance two cases of linkage in 35 pairs tested, and the failure to do so does not mean that certain of the pairs of characters may not subsequently be found to belong in one linkage group.

SYMBOLS

The following symbols will be used to designate the pairs of allelo-morphs considered in this paper:

I —dominant white	i —no inhibitor (of melanin)
h_e —cerebral hernia	H_e—normal skull
F —frizzled plumage	f —normal plumage
C_r—crest	c_r —no crest
W—white shanks	w —yellow shanks
R —rose comb	r —single comb
C —color (melanin)	c —recessive white

CROSSING OVER BETWEEN F AND I

In females. Backcross. Repulsion phase

It has long been known that the White Leghorn is a potentially colored bird in which pigmentation is inhibited by the dominant gene I. Fowls heterozygous for I are white but usually have a few feathers wholly or partially black. Frizzling has been shown by LANDAUER and DUNN (1930) and HUTT (1930) to be a unifactorial character dependent upon the domi-nant gene F. It is quite useful for linkage studies partly because hetero-zygotes are quite easily distinguished from both homozygotes and normal fowls, but also because the character is usually recognizable at two weeks or earlier.

In 1930, twelve females derived from a cross of colored frizzled females and White Leghorn male ($ff\,II\,CC$) were backcrossed to a White Orpington male. These twelve were thus of the constitution $\dfrac{Fi}{fI}\,CC$ and the Orping-

ton was $\dfrac{fi}{fi}$ cc. Since the females were homozygous for C, the recessive white introduced by the Orpington could not in any way complicate the 1:1 ratio of white to colored fowls expected from the segregation of I and i. Classifications were made at three weeks and in most cases were checked at four months. Both of the dominant characters are so distinct from their recessive allelomorphs that errors in classification are most unlikely. Red color was introduced by the twelve females, the dams of which were phenotypically frizzled Rhode Island Reds. Although this red is only partially inhibited by I, the presence or absence of the latter gene is easily recognized by the absence or presence, respectively, of black pigment in the wings and tail.

In the segregation of F and I in each of these twelve progenies (table 1) there is evident a distinct departure from the 1:1:1:1 ratio to be expected if the two genes were independent.

TABLE 1

Segregation of F and I in backcross, repulsion phase.

| | FRIZZLED | | NORMAL | |
FEMALE	WHITE FI	COLORED Fi	WHITE fI	COLORED fi
K 451	3	6	10	3
K 452	2	10	3	1
K 453	1	7	3	1
K 454	3	5	7	0
K 455	0	5	4	1
K 458	0	4	6	0
K 459	1	4	2	1
K 460	1	6	6	1
K 461	3	5	9	2
K 462	0	3	3	1
K 463	0	4	1	0
K 475	2	2	5	2
Unpedigreed eggs*	2	2	4	0
Totals	18	63	63	13

* Included because all females in the pen were of the same genotype.

While there are 81 frizzled to 76 normal and 81 white to 76 colored, a close fit to the expected 1:1 ratio in each pair, there is a marked excess in the Fi and fI classes with a corresponding deficiency in the FI and fi groups. Since F and I entered the cross in the repulsion phase, the segregation observed is to be expected if these two genes are linked. The birds in all four classes may be grouped as follows:

Parental combinations (Fi and fI):   126
New combinations (FI and fi):   31

Crossing over in this case is thus 19.74 percent.

In females. Backcross. Coupling phase

The only data available for this type of cross are those obtained from a mating made in 1932 of females having the genetic constitution $\frac{FI}{fi}$ to an Ancona male having the genotype *ffii*. Unfortunately only three females produced viable chicks so that the data are quite meagre. Classifications were made at two weeks and doubtful cases were re-examined at later periods. The numbers in the four possible classes were as follows:

Frizzled white	*Frizzled colored*	*Normal white*	*Normal colored*
FI	*Fi*	*fI*	*fi*
15	2	4	12

Parental combinations, *FI* and *fi*: 27
New combinations, *Fi* and *fI*   : 6

Considering that the numbers are small, the amount of crossing over —18.18 percent—is remarkably close to that found with larger numbers in the repulsion phase.

In the male. Backcross. Coupling phase

In 1932, A 1064, a white male proved to be heterozygous for frizzling and for dominant white, was backcrossed to twelve colored females having normal plumage. Subsequent segregation of *F* and *I* showed that these two genes were carried by the male in the coupling phase, so that the male was $\frac{FI}{fi}$ and the females *ffii*. The progeny were distributed as follows:

Frizzled white	*Frizzled colored*	*Normal white*	*Normal colored*
FI	*Fi*	*fI*	*fi*
39	5	8	30

Parental combinations (*FI* and *fi*): 69
New combinations (*Fi* and *fI*)   : 13

The amount of crossing over in the gametes of this male was thus 15.85 percent.

Other evidence of linkage of *F* and *I* was obtained in 1931 from the mating of L 15, a male heterozygous for frizzling, dominant white and color, to five colored females which were heterozygous for frizzling and color. All of these birds were from dams *FfIiCC* in constitution and were sired by a White Orpington. L 15's genetic formula was therefore $\frac{FI}{fi}$ *Cc* and the five females were $\frac{Fi}{fi}$ *Cc*.

The occurrence of recessive whites (*cc*) among the progeny of this cross

would at first sight appear to complicate any reading of the segregation of the I and i genes, but the theoretical expectations can be easily calculated.

The data are not suitable for the computation of the amount of crossing over, but the observed distribution can be compared with that expected on the basis of the linkage found in other matings. Although crossing over between F and I in females was 19.74 and 18.18 percent in repulsion and coupling phases, respectively, there is a possibility that linkage may be stronger in males than in females, and accordingly it would seem safer to assume for L 15 an amount of crossing over approximately the same as that found in the gametes of $\male$A1064, namely, 15.85 percent. Allowing for 16 percent crossing over between F and I and the independent segregation of I and C (BATESON and PUNNETT 1908, HADLEY 1914) the expected proportions of male and female gametes in this cross are as follows:

Male gametes		Female gametes	
FIC	21	FiC	25
FIc	21	Fic	25
fIC	4	fiC	25
fIc	4	fic	25
FiC	4	..	..
Fic	4	..	..
fiC	21	..	..
fic	21	..	..
	100		100

The theoretical distribution of phenotypes derived from these gametes and that distribution to be expected if there were no linkage are given in table 2 along with the actual frequencies in each class.

TABLE 2

Actual and theoretical distributions of the progeny of L15.

	FRIZZLED		NORMAL	
	WHITE*	COLORED	WHITE*	COLORED
Observed distribution	27	12	3	11
Expected (1) with 16 per cent crossing over between F and I.	28.2	11.5	4.9	8.4
Expected (2) with independent assortment.	24.8	14.9	8.3	5.0

For (1) $\chi^2 = 1.613$; $n=3$; $P=.66$
For (2) $\chi^2 = 11.343$; $n=3$; $P=.01$

* White fowls may be IC, Ic or ic.

By the application of the χ^2 test for goodness of fit it is found that the value of P for the fit to the expectation with independence is so small as to preclude the possibility of independent segregation of F and I in this cross. On the other hand the P value of 0.66 indicates a good fit to the expectation with 16 percent crossing over. It is recognized that this is only an approximate measure of the amount of crossing over which actually occurred, but the χ^2 tests do eliminate the hypothesis of independence and do indicate linkage.

From all the evidence for the linkage of F and I, summarized in table 3, it is clear that these two genes are in the same chromosome and that crossing over between them amounts to about 18 percent. The crossing over in a total of 272 measurable gametes is 18.38 percent; but in determining this figure the shortcomings of a result obtained by lumping together gametes of both sexes and having the genes in both the coupling and repulsion phases, are fully recognized.

TABLE 3

Summary of tests for linkage of F and I.

BIRDS TESTED	SEX	TYPE OF MATING	PHASE	GAMETES TESTED NUMBER	CROSSING OVER PERCENT
12 "K" females	♀	Backcross	Repulsion	157	19.74
3 other females	♀	Backcross	Coupling	33	18.18
A1064	♂	Backcross	Coupling	82	15.85
L15	♂	Partial backcross	Coupling	53	Approximately 16.00

ARRANGEMENT OF THE LINKED GENES

From the work of SUTTLE and SIPE (1932) it would appear that the genes for frizzling and crest are about 28 crossover units apart. So far as can be ascertained from their data, it is not clear that all the FfC_rc_r females used in their final crosses had the two dominant genes in the coupling phase. If some of these were $\dfrac{F\ c_r}{f\ C_r}$ and others $\dfrac{F\ C_r}{f\ \ c_r}$ (as seems possible from the fact that these birds were apparently two or more generations removed from the original frizzled, crested parent), the resultant distribution would not give a true measure of crossing over. However, since the percentage of crossing over in these females was almost the same as in a male which was evidently $\dfrac{F\ C_r}{f\ c_r}$, the data for the females are evidently valid, and it may be accepted that F and C_r are about 28 units apart.

This being the case, and the gene I being about 18 units from F, it follows that I and Cr should be either closely linked (about 10 units apart) or very loosely linked (depending upon whether I lies between F and C_r or to the left of both). In the latter case, the crossing over to be expected between I and C_r would be 46 percent, less whatever reduction would be caused by double crossing over. The only evidence so far available on this point is found in a small F_2 generation involving I and C_r reported by DUNN and JULL (1927) in which the segregation approached that to be expected if the genes were independent. The same authors mention (p. 32) a backcross of an IiC_rc_r male to Brown Leghorn females but report only the ratio of crested to non-crested among the offspring. If I and C_r were closely linked, the fact would surely have been noticed in this mating, whereas crossing over of more than 40 percent would have been almost indistinguishable from independent assortment except in larger numbers than they had. It therefore seems probable that I and C_r are very loosely linked and that F lies between them.

The data thus far available do not definitely establish the relationships between dominant white and cerebral hernia, but DUNN and LANDAUER (1930) have shown that the I and h_e are very closely linked. Unfortunately the expression of h_e is somewhat irregular in any but specially selected material so that it was impossible for these investigators to determine more exactly the linkage relations of the genes with which they worked. In one backcross in which the distribution indicates that h_e was fully expressed, crossing over between I and h_e was about 11 percent.

In consideration of the findings reviewed above and pending further data, it seems not unlikely that the four genes in this chromosome are arranged in the following order: I, h_e, F and C_r, and spaced somewhat as is suggested in figure 1. The gene h_e may be on either side of I.

It is desirable that some gene be located between F and C_r to permit working with shorter map distances in this region, and also that all the existing data be confirmed and extended. Experiments in these directions are in progress at this laboratory.
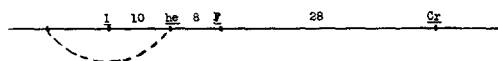

FIGURE 1.—Tentative arrangement of genes in the IFC_r chromosome.

GENES NOT IN THE IFC_r CHROMOSOME

To facilitate further progress in mapping the chromosomes of the fowl it is desirable to report all genes which have thus far been tested and found to show no linkage with those in the IFC_r chromosome. (Students of the genetics of maize have found it preferable to label the chromosomes

of that species by some distinctive gene or genes, rather than as chromosomes I, II, III, etc. For the present, their example seems well worth following.)

Rose comb (R)

In 46 progeny from two *FfRr* females backcrossed to an *ffrr* male the following distribution was found.

Frizzled rose	Frizzled single	Normal rose	Normal single
13	9	11	13

The numbers are small but the class frequencies suggest independence.

Better evidence that R is not in the IFC_r group was obtained indirectly by LANDAUER'S (1932) finding of no linkage between frizzling and creeper (table 6). Since creeper is very closely linked to R (LANDAUER 1931), the elimination of creeper should automatically eliminate R from this linkage group. It is therefore probable that the excess of parental combinations observed by DUNN and JULL (1927) in a backcross of rose, crested males to single, non-crested females (table 6) merely represented a chance deviation from the expected ratio. R and I were independent in their data.

White Shanks (W)

Evidence that F and W are independent was obtained in five matings involving these two genes (table 4).

Although the deviations from expectation in the totals for the backcrosses are fairly large, it seems likely that they arose from chance deviations in the progenies of the two males. In these some error may have been incurred by classifying some of the birds before maturity. The dis-

TABLE 4

Segregation of F and W in five matings.

TYPE OF MATING	FRIZZLED		NORMAL	
	WHITE SHANKS FW	YELLOW SHANKS Fw	WHITE SHANKS fW	YELLOW SHANKS fw
1. Backcross ♀♀ *FfWw* × ♂ *ffww*.	9	8	8	11
2. Backcross ♂ *FfWw* × ♀♀ *ffww*.	12	14	12	5
3. Backcross ♂ *FfWw* × ♀♀ *ffww*.	2	11	15	7
Totals	23	33	35	23
Expected with independence	*28.5*	*28.5*	*28.5*	*28.5*
4. F₂ observed	24	9	9	2
Expected with independence	*24.75*	*8.25*	*8.25*	*2.75*
5. Partial backcross, ♂ *FfWw* × ♀♀ *Ffww*	11	5	2	6
Expected with independence	*9*	*9*	*3*	*3*

tributions in matings 4 and 5 are based on adult classifications and fit the expectations fairly well. More data are desirable but so far these two genes appear to be independent.

This is confirmed by the independent segregation of dominant white and white shanks in reciprocal backcrosses and in a partial backcross (table 5).

TABLE 5

Segregation of I and W in three matings.

| TYPE OF MATING | WHITE* | | COLORED | |
	WHITE SHANKS W	YELLOW SHANKS w	WHITE SHANKS W	YELLOW SHANKS w
1. Backcross $\male IiWw \times \female\female iiww$	17	11	7	8
2. Backcross $\female\female IiWw \times \male iiww$	10	3	6	4
Totals	27	14	13	12
Expected with independence	*16.5*	*16.5*	*16.5*	*16.5*
3. Partial backcross $\male IiWwCc \times \female\female iiWwCc$	17	6	14	5
Expected with independence	*19.7*	*6.6*	*11.8*	*3.9*

* In mating 3 white fowls may be IC, Ic or ic.

If the excess in the IW class of the backcross progeny were accompanied by a corresponding excess in the iw group, linkage would be indicated, but the deficiency in the latter class (table 5) suggests that the excess of IW birds can be ascribed to chance or, more likely, to errors in classification. The distribution in mating 3 is based upon descriptions of adults and fits the expectation remarkably closely.

From these two sets of data it is evident that W is either not in the IFC_r chromosome, or, if it be present, too far removed from both I and F to show linkage with either of them.

Other Genes

Evidence that fourteen characters are independent of the IFC_r group is summarized in table 6.

As is to be expected, characters showing no linkage with one member of the group have also shown independence with other members of the IFC_r chromosome. It may be noted that the possibility that polydactyly belongs to this linkage group, as was suggested by DUNN and JULL (1927), is not excluded by the data thus far available. The combined backcross ratio of parental to new combinations when polydactyly was tested with dominant white was 213:186 and the corresponding ratio in trials with crest was 281:243. The question probably will not be settled till some gene is located to the left of I in the chromosome, so that the possibility

TABLE 6

*Characters apparently independent of the IFC_r group.**

LINKED GENE	TESTED WITH	INVESTIGATOR	EVIDENCE FOR INDEPENDENCE
I	Recessive white (or black)	BATESON and PUNNETT (1908)	Independence in 77 back-cross and in 67 F_2
I	Recessive white (or black)	HADLEY (1914)	Independence in 167 F_2
I	Rumplessness	DUNN (1926)	No linkage in 231 progeny
I	Rumplessness	WARREN (1932)	Backcross 84:104
I	Rose comb	DUNN and JULL (1927)	Independence in 170 F_2 Backcross 31:28
I	Rose comb	WARREN (1932)	Backcross 88:91
I	Pea comb	WARREN (1932)	Backcross 285:262
I	Polydactyly	SEREBROVSKY and PETROV (1930)	Backcross 52:37
I	Polydactyly	WARREN (1932)	Backcross 161:149
I	Creeper	SEREBROVSKY and PETROV (1930)	Backcross 96:80
I	Silky	DUNN and JULL (1927)	Independence in 93 F_2
I	White shanks	HUTT (this paper)	See table 5
I	White shanks	WARREN (1932)	Backcross 122:107
I	Leg feathering	WARREN (1932)	Backcross 157:137
I	Naked neck	WARREN (1932)	Backcross 304:308
F	Black	SEREBROVSKY and PETROV (1930)	Backcross 63:50
F	Blue	SEREBROVSKY and PETROV (1930)	Backcross 79:88
F	Split comb	SEREBROVSKY and PETROV (1930)	Backcross 33:40
F	Split comb	LANDAUER (1932)	Backcross 84:91
F	Rose comb	SEREBROVSKY and PETROV (1930)	Backcross 24:24
F	Rose comb	HUTT (this paper)	See page 89
F	White shanks	HUTT (this paper)	See table 4
F	Creeper	LANDAUER (1932)	Backcross 97:96
F	Naked neck	LANDAUER (1932)	Backcross 116:117
F	Mesodermal pigment	SEREBROVSKY and PETROV (1930)	Backcross 39:35
C_r	Silky	DUNN and JULL (1927)	Fair fit to independence in 62 F_2
C_r	Split comb	SEREBROVSKY and PETROV (1930)	Backcross 225:203
C_r	Pea comb	SEREBROVSKY and PETROV (1930)	Backcross 177:173
C_r	Rose comb	DUNN and JULL (1927)	Backcross 110:75
C_r	Rose comb	WARREN (1932)	Backcross 80:92
C_r	Rose comb	SEREBROVSKY and PETROV (1930)	Backcross 336:282
C_r	Blue	SEREBROVSKY and PETROV (1930)	Backcross 120:119
C_r	Black	SEREBROVSKY and PETROV (1930)	Backcross 222:215
C_r	White shanks	SEREBROVSKY and PETROV (1930)	Backcross 87:73
C_r	White shanks	WARREN (1932)	Backcross 107:115
C_r	Muff and beard	SEREBROVSKY and PETROV (1930)	Backcross 388:328
C_r	Rumplessness	WARREN (1932)	Backcross 112:122
C_r	Naked neck	WARREN (1932)	Backcross 125:107
C_r	Leg feathering	WARREN (1932)	Backcross 115:119
C_r	Polydactyly	SEREBROVSKY and PETROV (1930)	Backcross 160:130
C_r	Polydactyly	WARREN (1932)	Backcross 121:113

* The ratio given in backcross data is that of parental combinations to new combinations.

of polydactyly being near the extreme left end may be examined, unless the character be first found linked to some other which is definitely known to be independent of this group.

SEREBROVSKY and PETROV (1930) have reported a considerable number of linkage trials involving I, F, or C_r, but some of them had numbers too few to indicate either linkage or independence and for that reason not all of their data are included in table 6. Additional evidence that genes for leg feathering and mesodermal pigment are not in the IFC_r group was provided by DUNN and JULL (1927), chiefly in F_2 data. These workers also found several characters independent of cerebral hernia, but since h_e was somewhat irregular in its appearance in their stocks, and since DUNN and LANDAUER (1930) found it closely linked with I, it seems unnecessary to present their data. Genes independent of I are bound to be independent of h_e.

The association between crest and the trifid or multiple-point condition of the rose comb is well known. In 545 rose-combed birds raised by JULL (1930) from silky crosses, there were only 12 exceptions to the rule that crested birds had multiple point combs and non-crested fowls had single-spike combs. JULL concluded that the twelve had been incorrectly classified and that there is not close linkage between crest and some factor for multiple points but rather that the rose comb is modified by the gene for crest.

THE INFLUENCE OF SEX ON CROSSING OVER

To the best of the writer's knowledge, the first definite evidence that crossing over occurs in the female fowl was found by DUNN and LANDAUER (1930) in a backcross of $\dfrac{I\ H_e}{i\ h_e}$ females to an $ii\ h_e h_e$ male. This was to be expected in view of the previous finding by CHRISTIE and WRIEDT (1923) that crossing over occurs in the autosomes of the pigeon, which suggested that in birds female digamety is not a bar to crossing over as it is in the silkworm. The numbers observed in either of these cases were hardly adequate for the measurement of the effect of sex on crossing over in birds.

The data thus far available are not sufficient to permit conclusions about sex differences in crossing over in the fowl but it is of interest to note that males thus far tested have displayed slightly less crossing over than females. The figures are:

	Genes	Crossing over percentage	
		in ♂♂	in ♀♀
LANDAUER (1931)	C_p* and R	0.19 (2136)	0.68 (2347)
SUTTLE and SIPE (1932)	F and C_r	27.16 (81)	29.87 (77)
HUTT (this paper)	I and F	15.85 (82)	19.47 (190)
* Creeper.			

The numbers in parentheses give the number of gametes tested in each case. Pending further data it would appear that the effect of sex on crossing over is somewhat the same in the fowl as in the rat and the mouse. In these mammals crossing over is somewhat lower in the male than in the female.

If further data on crossing over in the two sexes of the fowl should confirm those given above, it would then be apparent that sex differences in crossing over do not depend upon heterogeneity of the sex chromosomes but upon other conditions associated with sex. In this connection it is of interest to point out that in the locust, Paratettix, and the crustacean, Gammarus, crossing over is also lower in males than in females, and that it is not found at all in the male of Drosophila. The absence of crossing over in the female silkworm is apparently at variance with the situation in other species thus far investigated.

SUMMARY

Crossing over between the genes for frizzling and for dominant white was found to be about 18 percent.

This finding along with those of other workers permits the tentative assignment to one linkage group of the genes for dominant white, cerebral hernia, frizzling and crest, and gives some idea of the arrangement of these genes in the IFC_r chromosome.

It was found that the genes for rose comb and for white shanks are not in this linkage group and the available evidence for the independence of other genes is presented.

Evidence that in the fowl crossing over is less in males than in females is considered and it is suggested that sex differences in crossing over may depend, not on heterogeneity of the sex chromosomes, but upon other conditions associated with sex.

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